Neotoma floridana (Ord, 1818)

Eastern Woodrat

Mus floridanus Ord, 1818:184. Type locality St. Johns River, Florida.

N[eotoma]. floridana Say and Ord, 1825:346. First use of name combination.

N[eotoma]. magister Baird, 1858:498. Type locality a cave near Carlisle, Cumberland Co., or near Harrisburg, Dauphin Co., Pennsylvania.

Neotoma pennsylvanica Stone, 1893:16. Type locality near top South Mtn., Cumberland Co., Pennsylvania, some 6 mi. from Pine Grove at a place known as Lewis' Cave.

Neotoma baileyi Merriam, 1894:123. Type locality Valentine, Cherry Co., Nebraska.

Neotoma campestris Allen, 1894:322. Type locality Pendennis, Lane Co., Kansas.

Neotoma attwateri Mearns, 1897:721. Type locality Lacey's Ranch, Turtle Creek, Kerr Co., Texas.

CONTEXT AND CONTENT. Order Rodentia, Family Muridae, Subfamily Cricetinae. The genus *Neotoma* contains approximately 22 extant species. Hall and Kelson (1959) distinguished four subgenera, with *N. floridana* assigned to *Neotoma*. Nine subspecies are currently recognized (Birney, 1973).

N. f. attwateri Mearns, 1897:721, see above.

N. f. baileyi Merriam, 1894:123, see above.

N. f. campestris J. A. Allen, 1894:322, see above.

N. f. floridana (Ord, 1818), see above.

N. f. haematoreia A. H. Howell, 1934:403. Type locality near summit Blood Mtn., 4,400 ft., Lumpkin Co., Georgia.

N. f. illinoensis A. H. Howell, 1910:28. Type locality Wolf Lake, Union Co., Illinois.

N. f. magister Baird, 1858:498, see above (*pennsylvanica* Stone is a synonym).

N. f. rubida Bangs, 1898:185. Type locality Gibson, Terrebonne Parish, Louisiana.

N. f. smalli Sherman, 1955:119. Type locality Key Largo, Monroe Co., Florida.

DIAGNOSIS. *Neotoma floridana* differs from all other species of woodrats with adjacent ranges in having the anterior palatal spine forked. It differs from *N. micropus* in less gray color, interorbital ridges straight, posterior margin of bony palate concave or notched, and sphenopalatine vacuities narrower; from *N. albigula* in larger size, skull more robust and arched, interorbital ridges straighter, and septum intact (maxillovomerine notch absent); from *N. mexicana* in larger size, throat and breast white to base of fur, skull more robust and arched, interorbital region wider and more ridged, maxillovomerine notch absent, posterior margin of palatal bridge concave or notched, sphenopalatine vacuities narrower, teeth larger, and anterior median fold of M1 shallow (Finley, 1958). *N. floridana* cannot easily be confused with *N. cinerea*, which has larger ears, bushy tail, fully furred sole of hind foot, and a skull with interorbital region narrowly constricted and channeled and with frontal and temporal ridges narrowly separated.

The genus *Neotoma* was last revised by Goldman (1910). More recently, the relationships of *N. floridana* have been studied by Schwartz and Odum (1957), Birney (1973, 1976), and Zimmerman and Nejtek (1977).

GENERAL CHARACTERS. This medium-sized, nocturnal rodent has soft pelage, large black, protuberant eyes, large and sparsely-haired ears, and a moderately long tail with short hairs (Fig. 1). Dorsal surfaces of adults are brownish-gray, tinged with various amounts of black. Sides are lighter brown, with some dark hairs interspersed. The ventral surface is white from the throat posteriorly to the tip of the tail. The dorsal portion of the tail is blackish-brown and contrasts sharply with the white below.

The head is generally the same color as the dorsal surface, becoming more grizzled in older animals (Rainey, 1956). In adults worn summer pelage becomes bright cinnamon-orange. A brown stain sometimes is found on the mid-ventral parts. Stains result from the activity of the ventral abdominal gland. The young are grayer than adults, particularly on the belly. Poole (1940a) noted that males and females were colored alike.

The front feet have four toes (Rainey, 1956), whereas the rear feet have five. All toes have well-developed, sharp, downward-curved claws; the feet have large pads. The vibrissae are long and may extend to a maximum length of 75 mm. The body is compact and muscular. The skin is thickened in older individuals of both sexes. Albinistic woodrats are known, but melanistic individuals have not been reported.

Rainey (1956) listed the external measurements of 48 adults (28 males, 20 females) from Kansas and indicated that males averaged slightly larger in most measurements. Standard measurements (in mm with range in parentheses) for males were total length 374 (305 to 450), length of tail 160 (130 to 180), length of hind foot 40 (35 to 42), and length of ear 26 (24 to 29). Average adult weights of 21 males and 14 nonpregnant females (in g with range in parentheses) were 299 (220 to 384) and 216 (174 to 260), respectively. In Louisiana, Neal (1967) recorded the average adult weight of 42 males as 277.1 g and that of 41 females as 247.9 g.

The dental formula for *N. floridana* is i 1/1, c 0/0, p 0/0, m 3/3, total 16. Hall and Kelson (1959) described the skull (Fig. 2) as follows: "Skull large, elongated; premaxillary tongues extending posteriorly beyond nasals; sphenopalatine vacuities relatively small; interpterygoid fossa broad; presphenoid constricted; auditory bullae relatively small, rounded; palate lacking posterior median spine; M1 with moderately developed anterointernal reentrant angle." Average cranial measurements (in mm with range in parentheses) from 46 skulls are: greatest length 50.6 (47.9 to 55.6), cranial breadth 19.2 (18.2 to 21.3), zygomatic breadth 26.2 (23.9 to 27.6), interorbital breadth 6.6 (6.1 to 7.4), length of nasals 19.2 (18.6 to 22.5), length of diastema 14.3 (13.0 to 15.6), palatilar length 20.0 (18.8 to 23.4), postpalatal length 19.4 (18.0 to 21.7) (Lowery, 1974).

DISTRIBUTION. The geographical range of *N. floridana* extends from central Florida north along the Appalachian Mountains to southeastern New York and Connecticut; westerly to southwestern Nebraska and eastern Colorado; thence south through Oklahoma and central Texas to the Gulf of Mexico (Fig. 3). Disjunct populations occur in north-central Nebraska (*N. f.*

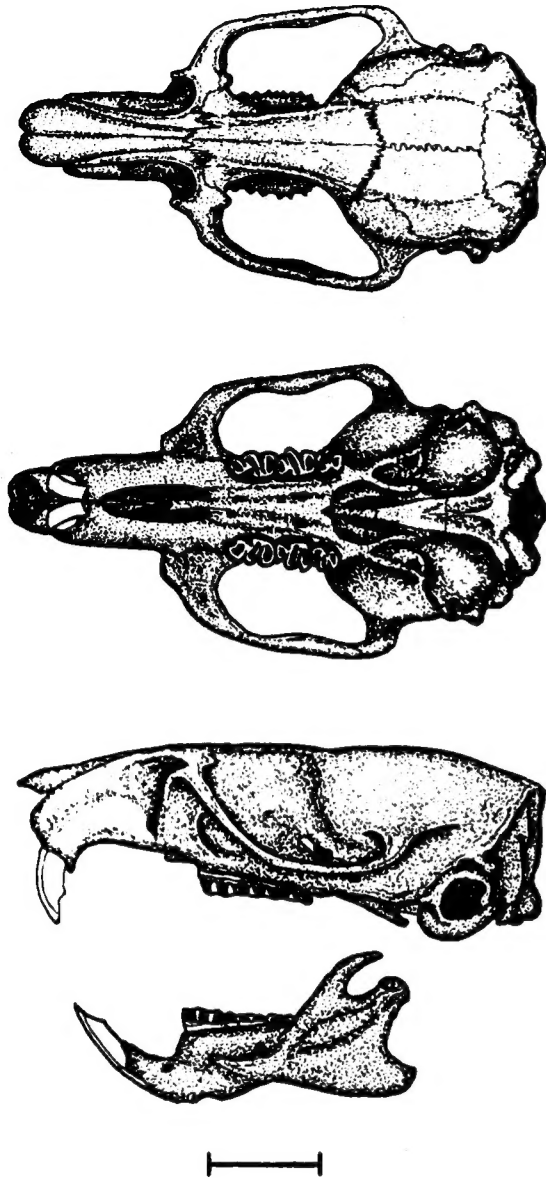FIGURE 1. Adult female *Neotoma floridana* from Bradley County, Arkansas.

FIGURE 2. Dorsal, ventral, and lateral views of the cranium and lateral view of the lower jaw of an adult female *Neotoma floridana* (ASUMZ 614) from Desha County, Arkansas. Scale represents 10 mm. Illustration by Renn Tumlison.
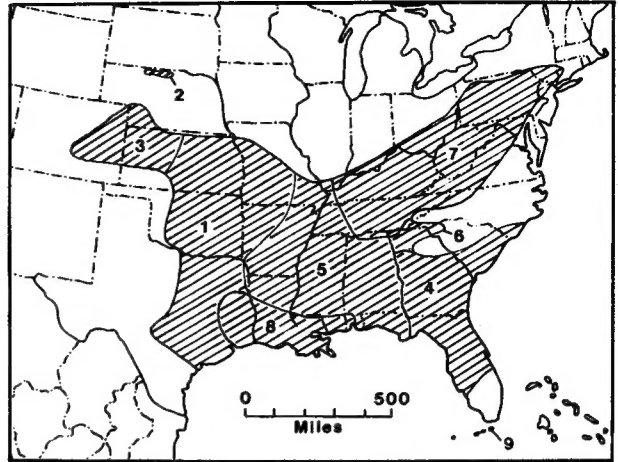

FIGURE 3. Geographic distribution of *Neotoma floridana* and subspecies (from Hall and Kelson, 1959, as modified for western subspecies by Birney, 1973): 1, *N. f. attwateri*; 2, *N. f. baileyi*; 3, *N. f. campestris*; 4, *N. f. floridana*; 5, *N. f. illinoensis*; 6, *N. f. haematoreia*; 7, *N. f. magister*; 8, *N. f. rubida*; and 9, *N. f. smalli*.

baileyi) and in Florida (*N. f. smalli*) on Key Largo (Birney, 1973; Hall and Kelson, 1959).

The greatest portion of the geographic range lies within the eastern deciduous forest, but it also extends into the grasslands of the Great Plains. In eastern Colorado eastern woodrats live under conditions of scanty rainfall and vegetation. On the Colorado plains, woodrats are adapted to the most arid conditions and coldest winters encountered by the species (Finley, 1958). The summers are hot and dry and the winters are cold. In Colorado, eastern woodrats occur only within the upper Sonoran Life-zone; the highest altitudinal record is 1,740 m (5,700 ft).

Bader and Hall (1960) found an old woodrat nest with cranial elements of *N. floridana* in an Indiana cave 80 km north of the present range. Poole (1940b) indicated the species was commonly found in Indian middens in Pennsylvania outside of its present range.

Neotoma floridana is the only member of the genus occurring in the eastern United States. At several localities in the western portion of its range it closely adjoins the ranges of other woodrats. Although the ranges of *N. floridana* and *N. micropus* come within close proximity over a large area, Spencer (1968) and Birney (1973) found only a single area of sympatry in western Oklahoma.

Finley (1958) found the range of *N. floridana* in close approximation with those of *N. albigula*, *N. micropus*, *N. mexicana*, and *N. cinerea*, but no contact zone was found. *N. floridana* and *N. albigula* were known to be sympatric at one locality on the Edwards Plateau (Texas) late in the 19th century (Birney, 1976).

FOSSIL RECORD. Birney (1973) and Genoways and Birney (1974) summarized some of the fossil history of the genus *Neotoma*. Birney (1973) indicated that the genus arose in late Miocene or early Pliocene. The ancestral stock evolved into the presently recognized subgenera by the beginning of the Pleistocene. *N. floridana* apparently evolved during the Pleistocene from a population isolated by the glacial advance. According to Zimmerman and Nejtek (1977) the divergence of *N. micropus* and *N. floridana* occurred during the first half of the Wisconsin, about 112,000 years BP. Hibbard (1941a, 1941b, 1967, 1970), Gidley and Gazin (1933, 1938), and Alvarez (1966) provided additional information on fossil species of woodrats.

FORM. Information on the gross anatomy of *Neotoma*, including external anatomy, myology, osteology, and the digestive and urogenital systems was summarized by Howell (1926). Sprague (1942) detailed the osteology and myology of the hyoid apparatus of *N. micropus* and *N. fuscipes*; the hyoid of *N. floridana* is no doubt similar.

Adults in fresh winter pelage (Poole, 1940a) are darker and grayer on the back due to a heavier mixture of fresh black guard hairs. The sides are more yellowish than those in summer pelage, but by March they become slightly more brownish; the black dorsal hairs simultaneously fade to a dull gray. This process of fading is continuous until the general tone of the back is much browner and more uniform. Ordinarily the molt progresses uniformly without developing a contrasting pattern between the worn and fresh areas.

Several investigators (Spencer, 1968; Rainey, 1956; Sands, 1951; Poole, 1940a) remarked about the ventral abdominal gland of *N. floridana*. The gland is present in both sexes (Spencer, 1968), but reaches its maximum development in males, where it is approximately 5 to 7 mm wide and 50 to 65 mm in length. In males, it increases in size during the breeding season and produces an exudate which stains the adjoining hairs a dark brown (Clarke, 1973). There is a positive correlation between testes weight and the size of the gland. In both sexes the gland is under the control of androgens. Males probably mark their houses with the gland exudate during the breeding season, which helps females to find mates.

The baculum of *N. floridana* was described by Burt and Barkalow (1942) and Burt (1960). It is short and the broad, proximal end has upturned lateral wings that make it U-shaped in cross section. In some there is a slight ventral concavity. From the proximal end the bone gradually tapers into a rounded shaft at approximately the midpoint. Average measurements (in mm)

of 10 bacula (including those of *N. f. magister*) listed by Burt and Barkalow (1942) were: length 6.70, dorsoventral depth (at base) 1.69, lateral width (at base) 3.08, dorsoventral depth (near midpoint) 0.74, and lateral width (near midpoint) 0.81. The baculum of *N. floridana* most closely resembles that of *N. micropus*. The phallus of *N. floridana* was described by Hooper (1960).

FUNCTION. The sense of smell is highly developed (Rainey, 1956) and hearing is extremely good. Vibrissae possess an acute tactile sense and help the animal move in the dark (Poole, 1940a).

Birney and Twomey (1970) studied the effects of NaCl on water consumption, weight, and survival in *N. floridana* and *N. micropus*. Somewhat surprisingly, the more xeric-adapted *N. micropus* drank both more tap water and saline water than the mesic-adapted *N. floridana*. Both species lost weight at a comparable rate; at the highest NaCl concentration only 20% of the *N. micropus* survived, whereas 43% of the *N. floridana* survived. The authors suggested the differences most likely developed in relation to food habits. *N. micropus* feeds year-round on succulent cactus (*Opuntia*); thus there is little need to withstand desiccation. *N. floridana* must endure "dry" periods (especially winter) when free water is frozen and succulent foods are unavailable; thus it is adapted to survive on limited moisture supplies.

ONTOGENY AND REPRODUCTION. Copulatory behavior of *N. floridana* was observed by Pearson (1952), Hamilton (1953), Knoch (1968), Spencer (1968), Dewsbury (1974), and Kinsey (1976). Fights among paired woodrats frequently result in the death of one member. Birney (1973) found that certain breeding pairs were more compatable than others. If the female became dominant fighting occurred, and if not separated the male was usually killed. If the male established dominance, fighting was generally of short duration and pairings frequently resulted in the production of offspring. Hamilton (1953) noted that when a female was placed in a male's cage, he would quickly attempt to mate. He would drum his hind feet and sniff at the perineal region while following the female. The female would soon become docile and assume a position signalling her readiness for copulation. If mating did not occur immediately, she would follow the male, licking at his scrotum. Eventually, copulations ensued. Dewsbury (1974) indicated that the male mounts from behind and after rapid, shallow thrusts gains penetration. Intromission immediately followed, and was indicated by cessation of pelvic thrusting. Following intromission, the female often moved away with the male still coupled by a copulatory lock. A mean of 4.4 copulations (range, 2 to 6) occurred in mating trials, with a mean duration of 47.8 (range, 4 to 117) seconds per copulation. Woodrats are polyestrous; estrous cycles usually last for periods of 4 to 6 days (range, 3 to 8) (Asdell, 1964). Birney (1973) attempted use of activity wheels to determine breeding readiness. Activity peaks indicated 3 to 6 day estrous cycles, but the method did not provide a degree of accuracy to be of use. Chapman (1951) described the estrus of captive woodrats.

The gestation period, determined from five matings, varied from 33 to 35 days (Knoch, 1968). Spencer (1968) reported a gestation period of 35 days for two matings. Birney (1973) found no distinct difference in the gestation periods of *N. floridana* and *N. micropus*; apparently they range from 32 to 38 days with a modal duration of 35 days. Murphy (1952) observed muscular contractions in the abdominal region of a female prior to parturition of a second offspring. Her back was extremely arched and her hind feet were slightly parted and extended well forward. Her body was supported by the hind feet and tail, which formed a tripod. The front feet were held off the substrate, and the head was bent downward with the eyes closed. Following birth, the young was licked clean. It then attached itself to a teat, where it remained during births of two siblings. The afterbirth was eaten by the mother. Following parturition, the skin in the mammary area of the nursing mother was thickened, wrinkled, and void of hair; the teats were soft and extremely long (Rainey, 1956).

A literature survey by Rainey (1956) indicated litter size varied from one to six, with a mode of two. Counts (n = 50) of embryos and placental scars by Goertz (1970) indicated a mean litter size of 3.2 (range, 1 to 7). The breeding season appears to vary geographically. Females breed from March through October (Goertz, 1970) in Oklahoma, whereas in Kansas (Rainey, 1956), most breeding occurs from February through August. In Florida (Pearson, 1952; Hamilton, 1953) and coastal Georgia (Golley, 1962), *N. floridana* apparently breeds throughout the year. In the mountains of Georgia, reproduction was curtailed in December,

January, and February (Golley, 1962). Schwartz and Schwartz (1959) stated that two to three litters are born annually. Females mate soon after giving birth, and litters can follow in succession.

Newborn young have weak and unsteady movements (Pearson, 1952). The skin has a chapped and scaly appearance. Hair 1 mm in length is present on the dorsal surfaces, but is hardly noticeable on the venter. The dorsum is darkly pigmented (Worth, 1950), and the tail is slightly bicolored. Claws are present. The eyes and ears are closed (Svihla and Svihla, 1933); the pinnae are folded over the ear openings. The incisors project through the gums; a diamond-shaped opening between the upper and lower incisors provides space for the mother's teat, which the young hold tenaciously. The vibrissae are prominent, measuring approximately 5 mm in length (Hamilton, 1953). Measurements (in mm) of 21 young taken a few hours after birth (Hamilton, 1953) were as follows: total length, 87 to 96; length of tail, 24 to 27; and length of hind foot, 13.5 to 14.8; weight, 11.8 to 14.1 g. Sounds are limited to sucking sounds and occasional squeaks. The four mammae are evident in newborn females. The female releases her young from her teats by placing a foot on a young and turning repeatedly in a small circle. The ears unfold in about 9 days and the eyes open in 15 to 21 days (Schwartz and Schwartz, 1959). The young are weaned in about 4 weeks. Hamilton (1953) presumed that at 70 days they were independent. In a captive litter of five, Fitch and Rainey (1956) found the average weight gain was 1.5 g per day during the first 2 months, and somewhat less in the third month. At 3 months of age, the average weight was 120 g, with males consistently outweighing females. Thereafter, the rate of increase slowed (Rainey, 1956); full adult weight was not attained until 8 months. Woodrats weighing less than 150 g when first captured gained an average of 1.32 g per day (Goertz, 1979). Adults fluctuate in weight to some extent, but reasons for this are not clear (Rainey, 1956). Adult males reach their peak in weight at the beginning of the breeding season (February and March) and decline to a low point in May. There is a rapid recovery in June, and a slight decline during hot weather in late summer and early fall, as activity increased. Weight steadily increases again in late autumn and winter.

The young first molt when 5 to 6 weeks old. Molt starts on the abdomen, chest, and throat, and progresses dorsally (Rainey, 1956). The second molt immediately follows the first.

In females, puberty is reached at 5 to 6 months of age, or at a weight of about 160 g (Asdell, 1964); however, puberty is delayed in animals reaching this age during the winter. Early-born young may breed the same year. Fitch and Rainey (1956) noted that individuals which breed the same year do so in late summer or early autumn. Birney (1973) captured a subadult *N. f. baileyi* in late August which was nursing three young. In most cases however, sexual maturity is not attained until the spring of the year following that in which they were born (Rainey, 1956). Males are not known to attain sexual maturity their first season although they may by February or March of the following year.

Woodrats have a long life expectancy in comparison to other small rodents. One female, already an adult when marked, was still alive 991 days later (Fitch and Rainey, 1956). Within 1 year of their initial capture, however, 95% of the woodrats marked by Goertz (1970) disappeared from the study areas.

ECOLOGY. *Neotoma floridana* is primarily an eastern woodland species, but occupies a variety of habitats, including lowland hardwood forests (Neal, 1967), marshes (Svihla and Svihla, 1933), mountains (Poole, 1923; Howell, 1933; Coleman, 1949), coastal plains (Cross, 1955), swamps (Chamberlain, 1928; Hamilton, 1953), and grasslands (Finley, 1958; Wiley, 1971).

Woodrats build large escape houses, which provide escape from predators and offer protection from extremes of temperature and moisture. In Oklahoma, Murphy (1952) observed that houses varied widely in size and in the sites chosen for their construction. Houses were usually built under projecting rock outcrops where only the entrances could be seen. At times, houses were built in brush piles, at the base of large trees, in tangles of briars, and occasionally in trees. Some houses were as large as 4 m in length by 2 m in width, and over 1 m high. Svihla and Svihla (1933), Goodpaster and Hoffmeister (1952), Jones (1964), and Birney (1973) noted that woodrats use abandoned buildings for house sites. In southern Missouri, limestone bluffs were densely inhabited by woodrats (Leopold and Hall, 1945). In swampy areas in central Florida, houses were usually built under willow trees on high ground (Hamilton, 1953). In eastern Kansas, hilltop limestone outcrops were most heavily relied upon for house sites, although the bases of osage orange (*Maclura pomifera*) were also commonly used. Habitat requirements and house location of the

western subspecies of *N. floridana* have been described by Birney (1973). He indicated the prime component of habitat was the availability of cover, which offers materials and sites for house construction.

The shape of the house depends on its location (Rainey, 1956). If a vertical object is available for support, the house will be cone shaped; if no support is available, the house will tend to be flattened and its base will be broader. A typical house is 1.2 m in diameter and about 1 m high (Hall, 1955). Houses are constructed primarily of twigs and sticks as large as the woodrat can carry (Rainey, 1956). New woody vegetation is added in season; attached leaves tend to fill the spaces between the sticks. Practically anything in the vicinity that is transportable is used to make up the house. Houses are partially constructed of bones, rocks, dried dung, and any other material (Murphy, 1952). Poole (1940a) provided an extensive list of materials associated with houses. In Colorado, Finley (1958) found that *N. floridana* utilized a wide variety of natural shelters and shelter materials. When preferred rock shelters were unavailable, they built houses practically everywhere. These capabilities enable woodrats to inhabit portions of the High Plains where resources are sparse.

A typical house contains two or more nests (Hall, 1955). The nests are usually at the center (Murphy, 1952). They are nearly spherical and measure about 205 mm in diameter. Dry grasses, shredded bark, and occasionally feathers are used in nest construction. A woodrat prepares material for the nest by shredding and fluffing it with its teeth. The woodrat then shapes and lines the nest by turning in circles and simultaneously making quick motions of the head and forefeet (Poole, 1940a).

Houses are surrounded by wide, smooth paths clear of debris (Finley, 1958) but bordered by midden materials. Most of the midden materials are pushed outside of the cleared path, forming a distinct shoulder. From this ring path, two or more side paths lead away from the house to adjacent areas. Rainey (1956) thought that if a house is destroyed and the woodrat does not soon find other shelter, it probably is captured by a predator. A house is used yearlong and sometimes for the life of the animal, who continually adds to the structure (Schwartz and Schwartz, 1959).

Of the 105 woodrats studied in a live trapping program by Rainey (1956), 44.7% were females and 55.3% were males. Goertz (1970) reported a nearly equal sex ratio (142 males, 139 females). Neal (1967) calculated the population density of woodrats by the strip census method. Active houses were counted. Assuming one woodrat per house, he estimated 0.82 woodrats per ha in 1965 and 0.20 for 1966. The decline in 1966 was attributed to poor acorn crops in 1964–65. During several years of study, Fitch and Rainey (1956) recorded similar declines in woodrat populations. They attributed these to extremely cold weather and heavy accumulations of snow and ice.

In eastern Kansas, five species of predators cause the greatest mortality to woodrats (Fitch and Rainey, 1956). They are the great horned owl (*Bubo virginianus*), the spotted skunk (*Spilogale putorius*), the long-tailed weasel (*Mustela frenata*), the pilot black snake (*Elaphe obsoleta*), and the timber rattlesnake (*Crotalus horridus*). The pilot black snake and the long-tailed weasel appear most formidable because their size allows them to enter the house. The timber rattlesnake is probably less effective because it lies in wait for its prey, and is not so apt to enter houses. The stomachs of 70 timber rattlesnakes and 15 copperheads (*Agkistrodon contortrix*) from Pennsylvania and New Jersey had no remains of woodrats (Poole, 1940a). There were however, woodrat remains in a great horned owl pellet.

The most conspicuous ectoparasites of eastern woodrats are warble (bot) fly larvae of the genus *Cuterebra* (Murphy, 1952; Lay and Baker, 1938; Rainey, 1956; Neal, 1967). The larvae are found beneath the skin, most generally on the throat, and when fully developed may form a cyst about 15 mm in diameter. Of 105 woodrats examined by Rainey (1956), 16.2% were infected. Infestation was highest in dry years and peak infestation occurred in July and August. Infected animals seemed to show no discomfort from the larva. Of 92 woodrats collected in Louisiana (Neal, 1967), 4.2% were visably infected by *Cuterebra* larvae. Beamer et al. (1943) described the biology of the woodrat cuterebrid, *Cuterebra beameri*, in Kansas.

Murphy (1952) reported fleas, ticks, and mites as common ectoparasites of eastern woodrats. Ticks and mites were of the genera *Ixodes* and *Eutrombicula*, respectively. Fleas were of the family Dolichopsyllidae. *Conorhinopsylla nidicola*, *Epitedia wenmanni*, and *Orchopeas sexdentatus* were fleas found on *N. floridana* by Rainey (1956). He noted that more male woodrats were infested than females, and infestations occurred yearlong, but

were less severe in wet years. Rainey (1956) found that chiggers were the most numerous ectoparasites; the genera *Trombicula*, *Euschongastia*, and *Pseudoschongastia* were represented. Chiggers, grouped in clusters, were found in all months of the year. The most common places of attachment were in the ears, at the base of the teats, around the vaginal orifice, around the anus, and on the scrotum. Although infestations were never heavy, nymphs and larvae of the American dog tick (*Dermacentor variabilis*) were found on the woodrats. Ticks occurred on the muzzle and in the ears, and were found on woodrats only during the summer months.

Endoparasites of eastern woodrats were described by Murphy (1952). The nematode *Longistriata neotoma* infected 20% of the animals. The most common helminth was *Bohmiella wilsoni*, which infected 34%. Of two sexually mature cestodes collected, one was identified as *Andrya* sp. The hepatic tissue of four animals contained cestode larvae, *Taenia taeniaeformis*. In Colorado, members of the families Laelaptidae, Trombiculidae, Haematopinidae, Hystrichopsyllidae, and Ceratophyllidae infected eastern woodrats (Finley, 1958). Additional parasites are reported from *N. floridana* in Alabama (Zambernardi, 1956), Kansas (Jellison, 1945), and Louisiana (Neal, 1967). The protozoans *Eimeria glauceae* and *E. dusii* have been described from Alabama woodrats (Wheat and Ernst, 1974). Bubonic plague occurs in wild woodrats (Schwartz and Schwartz, 1959).

The individual rat's house was found by Fitch and Rainey (1956) to be the base of operations for an eastern woodrat; home ranges were altered over periods of time. Increased sexual activity, voluntary wandering, and attraction to a specific food supply not available near their houses led to sporadic movements of woodrats out of their main areas of activity. Since most trails could not be traced for more than 10 m from the house, most foraging probably occurred within a short distance. Live trapping records indicated that woodrats foraged within 21 m of the house.

Tate (1970) found that mean home range (in square meters) for eight adults was 2,127 for circular range method, 662 for minimum area method, and 260 for modified minimum area method. Adult males had larger home ranges than adult females, whereas the home ranges of subadults of both sexes were larger than adults. The longest moves were 68 m for an adult male, and 54 m for an adult female. Goertz (1970) calculated a home range of 0.26 ha for males and 0.17 ha for females.

In Texas, Lay and Baker (1938) recorded that 87 m was the longest distance a woodrat traveled; 11 m was the shortest distance. One animal occupied a home range of only 25 m in diameter. The home ranges of many woodrats living along a gully 185 m in length overlapped. Pearson (1952) found the greatest distances between points of capture averaged 55 m with extremes up to 165 m. Fitch and Rainey (1956) recorded a mean maximum distance of 105 m for 27 adult males, and 44 m for 39 subadult and adult females. Extremes for males were 0 and 330 m and for females, 0 and 200 m. The longest moves were made by large males in breeding condition. Ireland and Hays (1969) used marked tinfoil balls to determine home range size of eastern woodrats. According to Fitch and Rainey (1956), the overlap in home ranges and the intolerance between individuals tends to form a minimum interval between houses. They believed this spacing probably prevents depletion of the food supply and overcrowding.

Lay and Baker (1938) showed that woodrats have some homing ability. Of three they released in woodland 185, 305, and 405 m from their home range, all returned. Five individuals released one-half mile away in pasture did not return. Classen (1968) displaced 87 marked animals 130 to 1,173 m from their home areas. Of these, 49 returned home. Seventy-four percent of those displaced less than 305 m returned, whereas only 32% displaced over 305 m returned. Success in homing was highest in males. Homing was attributed to nonrandom movements through familiar terrain.

Woodrat houses are used as shelter by many other animals which live in close proximity to woodrats. Fitch and Rainey (1956) found snakes, lizards, toads, and small mammals associated with woodrat houses. The eastern cottontail (*Sylvilagus floridanus*) and the woodland white-footed mouse (*Peromyscus leucopus*) were the most frequent inhabitants, especially of abandoned houses. The opossum (*Didelphis virginiana*) occasionally used vacated houses. Rainey (1956) found white-footed mice to be the most important competitors for food; in rocky areas they were the most numerous cohabitants. Additional animal associates were listed by Lay and Baker (1938) and Murphy (1952).

Schwartz and Schwartz (1959) stated that woodrats consume

only about 5% of their weight in dry matter each day. In summer months, most feeding was done while foraging; only small amounts of food were brought back to the house for daytime feeding (Rainey, 1956). Food preferences vary and the food favored by one population may not be used by a population in a different locale. Grasses are rarely eaten and are probably an insignificant part of the diet (Rainey, 1956). Finley (1958) indicated that no single species of plant provides the bulk of the food. Rainey (1956), however, found that a few species of plants may make up the greater part of the diet. He listed 32 plant species utilized by woodrats. Osage orange was by far the most important food; both leaves and fruit provide food all year. In Texas, pecans are heavily used for food (Strecker, 1929). In Tennessee, Goodpaster and Hoffmeister (1952) found houses filled with seed pods of honey locust (*Gleditsia triacanthos*), mint (*Mentha* sp.), acorns (*Quercus* spp.), and beechnuts (*Fagus grandifolia*). Newcombe (1930) found large amounts of mushrooms at nest sites in Pennsylvania, but it was not known if they were eaten. In Oklahoma, the diet is almost entirely plants; animal matter is only rarely consumed (Murphy, 1952). Only three of 55 stomachs examined contained animal material. Acorns, sumac fruit and bark (*Rhus* sp.), poison ivy (*R. toxicodendron*), redbud (*Cercis canadensis*), dogwood (*Cornus asperifolia*), and Kentucky coffee tree (*Gymnocladus dioica*), constituted the main foods. Acorns were stored and made up the chief winter food in that area. Woodrats also make extensive use of acorns in Louisiana (Neal, 1967). Finley (1958) gave an extensive list of foods utilized by the species in Colorado, where food habits were locally variable. Additional notes on food habits were reported by Lay and Baker (1938), Poole (1940a), and Heisler (1941).

Gnawed bones are often found in the midden piles associated with houses. Poole (1940a) believed the bones were used to sharpen the teeth and provide mineral nutrients.

Murphy (1952) stated that drinking water is apparently not needed, although individuals in captivity will drink readily if it is available. He found that during periods of drought many houses were located so far from standing water that woodrats must have obtained it from dew or succulent vegetation, or survived on water obtained from metabolism of foods. Apparently most of the water requirements of wild woodrats were satisfied by eating succulent vegetation. Newcombe (1930) estimated approximately 100 cc of water was consumed every 48 h.

BEHAVIOR. Eastern woodrats are basically solitary (Murphy, 1952). Each occupies the house it built and lives there alone, except during the breeding season and when raising offspring. Woodrats are active throughout the year, although in times of wet weather or extreme cold they probably stay in their houses. Woodrats are primarily nocturnal, but at times they move about in late afternoon. In the laboratory, they sleep most of the day and show the greatest activity during the first hours of darkness. Wiley (1971) found that woodrats become active about 30 min before total darkness and continue foraging until 30 min before sunrise. Seventy-five percent of total activity occurred before midnight with 54% occurring between 2030 h and 2230 h. Zervanos (1969) found that activity periods in the laboratory began soon after lights out and ceased a few hours before lights on. Light/dark interchange was found to be a strong synchronizer of activity. Schwartz and Schwartz (1959) noted that young were bolder than adults and were more apt to move about in the daylight. Rainey (1956) found woodrats were more active on dark rainy nights than on clear ones. Woodrat activity was low on nights when the moon was full or nearly so, and high during new and quarter moon phases (Wiley, 1971). Tate (1970) found trapping success was 35% higher on cloudy nights than on clear nights.

By the use of red light at night Finley (1959) and Wiley (1971) observed woodrats grooming, foraging, and traveling over habitual routes between houses and feeding areas. Though shy of moonlight and easily frightened by sound, they were usually undisturbed by red light. Zervanos and Davis (1968) indicated that woodrats were able to perceive red light.

A captive reproductive population, composed of a female, her offspring, and the offspring resulting from their interbreeding was established by Kinsey (1977). The colony consisted of dominant individuals which lived in and defended nest sites, and subordinate individuals which lived in communal aggregations. The latter avoided encounters with the territorial individuals. Membership into either group appeared dependent on age, sex, season of the year, and availability of nest sites. Agonistic interactions demonstrated a seasonal pattern of occurrence among

adults. Females defended territories and were aggressive during the spring and summer months, whereas in the fall and winter males became aggressive and established territories.

In another study, Kinsey (1976) found low density populations (two to four adults/65 m² cage) of *N. floridana* to exhibit despotic social organization in which one alpha rat killed or wounded all other group members. In five of seven high density populations (six to 14 adults/9.5 m² cage) dominance hierarchies and high levels of social interaction were established. Two unisexual populations remained disorganized and only one individual survived in each.

When not alarmed, a woodrat rests by sitting on the rear feet and base of the tail, with the abdomen usually touching the ground; both front feet are generally placed on the ground; the ears are relaxed but do not lie flat (Rainey, 1956). On alert, the pupils of the eyes dilate, the ears are directed forward, the vibrissae are set in motion, and the body is held tense. Worth (1950) stated that woodrats spend most of the day sleeping very soundly. They generally sleep bent over with their head tucked between the front legs. The tail is curled partially around the body.

On open ground juveniles run erratically with the head held low (Rainey, 1956). Woodrats move in rapid dashes with alternating short pauses. In the dark they have been observed to enter extremely small openings while running at full speed. When climbing on a vertical surface, they rely on speed and momentum to some extent. They are proficient climbers, but have never been observed to climb by moving slowly. The large fleshy feet (Poole, 1940a) are well adapted for climbing and provide traction on vertical surfaces. The tail is a useful balancing organ and is carried in a fully extended and horizontal position when the animal is walking or running. When excited, the tail is carried higher and may be lashed from side to side. While fighting or feeding, the animal may stand upright and use the tail as a brace.

Woodrats are sanitary animals (Poole, 1940a). They place scats in piles up to 450 by 250 mm in extent and 50 mm deep. Scat heaps are often placed in the most exposed areas and some latrines seem to be used by several individuals over a period of time. In captive animals, three to 84 fecal pellets are voided each 24 h. Conspicuous dark stains from 150 to 200 mm in diameter in rocky areas were found to be urinating spots (Schwartz and Schwartz, 1959).

Woodrats give meticulous care to their pelage (Rainey, 1956). Underparts are cleaned while the rat rests on its hind legs and base of the tail. The front feet are used to part the hairs, and cleansing occurs by licking. The loose skin is stretched by the front feet so areas that are hard to reach may be cleaned. In order to clean the face the front feet are licked and rubbed over the face in a circular motion. Even the tail is cleaned thoroughly. Captive individuals have been observed to bend the head between the rear legs and clean the anal area after defecating. Dust baths are thought to be taken periodically, but are rarely observed.

Woodrats store food beginning in September or October (Rainey, 1956). Storing behavior is instinctive and, once started, it dominates all other activities. Foods are stored in compact bundles in galleries near the top of the house. Leaves stored in autumn will remain green until spring, but dry out during the summer.

Woodrats are intolerant toward each other (Poole, 1940a). In the wild, chasing and fighting occurs, especially when food is involved. Many captured specimens are scarred with torn ears and injured tails. The sex of an individual seems to make little difference in fighting, and when both sexes are involved, the female is usually the aggressor. When on guard prior to fighting, they squat on their hind legs and raise their front feet with the toes clinched (Lay and Baker, 1938). The head is held close to the shoulders and raised slightly. The ears are alternately raised and lowered. The vibrissae are directed forward and move rapidly from time to time. The lower jaw is moved from side to side producing a grating sound and the feet are thumped on the substrate. Most of the actual fighting is accomplished with jabs to the head with the front feet. The common mode of defense is by use of the front feet (Poole, 1936); the teeth are used only as a last resort.

Courtship seems to be limited to a mild form of "fighting" in which light blows are exchanged with front feet (Poole, 1940a). In captive breeding, male dominance was followed by some fighting, and an eventual high success rate in litter production (Birney, 1973). However, if the female became dominant, the usual outcome was the death of the male if the pair were left together.

Poole (1940a) stated that woodrats seldom make noises though they squeal when fighting or injured. They can grate their
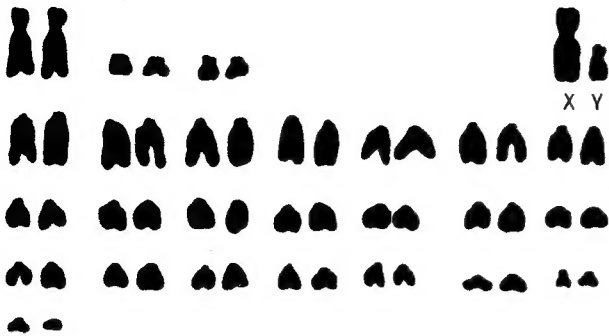
FIGURE 4. Karyotype of male *Neotoma floridana* from near Stillwater, Oklahoma (courtesy of Robert J. Baker).

teeth to produce a chattering sound. The thumping sound produced by the hind feet is familiar to all who have studied woodrats. It is apparently a response to fear or anger.

When escaping from their houses, woodrats follow predetermined routes (Rainey, 1956). If closely pressed by an enemy, they readily take to trees. When released in unfamiliar territory, woodrats are slow to react and act confused, but in familiar surroundings their movements are quick and direct. Black (1936), Worth (1950), and Svihla and Svihla (1933) observed females escaping from houses with the young attached to their teats. This behavior may be a valuable asset to the species in saving the young from danger.

GENETICS. The karyotype of *N. floridana* (Fig. 4) was described by Cross (1931), Matthey (1953), and Baker and Mascarello (1969). The autosomes consist of one large and two small pairs of distinctly biarmed elements and 22 pairs of graded acrocentrics ranging in size from large to small (2n = 52, FN = 56). The X is a large submetacentric and the Y is a medium-sized subtelocentric. Baker and Mascarello (1969) indicated that the karyotype of *N. floridana* is most similar to the most common and widely distributed karyotype of the polymorphic *N. micropus*. Both species have a similar graded series of 22 pairs of acrocentric chromosomes. However, Birney (1973) noted that all of the larger acrocentrics of *N. floridana* have a small amount of chromatin visible beyond the centromere, opposite the arm, whereas chromatin in *N. micropus* is only rarely located in this position on corresponding chromosomes.

Birney (1973) found *N. floridana* to be polymorphic in relation to the number of large biarmed chromosomes. In *N. f. baileyi*, the two biarmed autosomes are replaced by acrocentrics. He discovered a submetacentric Y chromosome in *N. f. baileyi* and in some populations of *N. f. attwateri* and *N. f. campestris*. A submetacentric Y was not found in the study of the populations *N. f. attwateri* and *N. f. floridana* by Baker and Mascarello (1969). Birney (1973) suggested that the karyotype with the greater number of biarmed autosomes is probably the one from which the others evolved.

Birney and Perez (1971) and Birney (1973) reported on the multiple hemoglobins of *N. floridana*, *N. micropus*, and their hybrids. Zimmerman and Nejtek (1975, 1977) studied the electrophoretic patterns of hemoglobin and albumin variation in *N. floridana* and several other species.

REMARKS. The *floridana* species group, as delimited by Birney (1976), contains *N. floridana*, *N. micropus*, *N. albigula*, and several Mexican species of restricted distribution. Birney suspected that further study might show that *N. f. magister* is a distinct species. Anderson (1969) noted the close relationship between *N. floridana*, *N. micropus*, and *N. albigula*, and suggested that the possibility of conspecificity needs further study. From a study of the phallus, Hooper (1960) felt the three species might be either conspecific or sibling species. Although *N. floridana* and *N. albigula* did occur together at one locality on the Edwards Plateau late in the 19th century, they apparently did not hybridize (Birney, 1976). An area of sympatry in west-central Oklahoma between *N. floridana* and *N. micropus* has been extensively investigated (Spencer, 1968; Heist, 1970; Birney, 1973). Although natural hybrids occur in the area of sympatry and laboratory hybrids are readily produced, Heist (1970) and Birney (1973) concluded that both populations are best recognized as distinct species. Electrophoretic data (Zimmerman and Nejtek, 1977) place the divergence of *N. albigula* from the parental form at approximately 155,000 years BP, i.e. during the late Sangamon

interglacial or early Wisconsin glaciation. *N. floridana* and *N. micropus* diverged more recently, perhaps during the first half of the Wisconsin approximately 112,000 years BP.

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